ERRATA.

'PHIL. TRANS.,' B, 1892.

P. 92. In explanatory note at foot of table *for* "Slight, indicates that . . ." *read* "? Slight, indicates that . . ."

P. 101. In column "Dog (2)" *for* "Pallor $<$ I" *read* "Pallor $>$ I."

P. 309, line 1, *for* "4" *read* "2"; line 2, *for* "37° à 41°" *read* "38° à 40°."

IV. *On the Origin from the Spinal Cord of the Cervical and Upper Thoracic Sympathetic Fibres, with some Observations on White and Grey Rami Communicantes.*

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[Plates 9, 10.]

IN the course of experiments already published on the origin from the spinal cord of the sweat-fibres for the fore-foot, and of the pilo-motor fibres for the face and neck, I had occasion to stimulate, in the spinal canal, the lower cervical and upper thoracic nerves. Whilst doing so I paid attention to the occurrence or non-occurrence of effects other than those with which I was at the time most concerned. Since the results were in many cases not in accordance with the statements of earlier observers, it seemed to me desirable to determine as many as possible of the "sympathetic" effects, which can be produced by stimulation of each of the lower cervical and of the upper thoracic nerves.

In giving the results of my experiments it will be convenient to take separately, and in order, the origin of (1) the fibres causing dilation of the pupil, opening of the eyelids, and retraction of the nictitating membrane; (2) the vaso-constrictor and vaso-dilator fibres of the head; (3) the secretory fibres of the salivary glands; (4) the accelerator fibres of the heart; and (5), and more briefly, the remaining efferent fibres of the sympathetic region in question. Having dealt with the origin of the various classes of nerve fibres, I shall consider some points with regard to white and grey rami communicantes, points which naturally arise out of GASKELL's work on visceral nerves.

The experiments were made upon Dogs, Cats, and Rabbits, most experiments being made on Cats and fewest on Dogs.

In all cases anæsthetics were used; with Dogs, morphia was first injected subcutaneously, and later a mixture of equal parts of absolute alcohol, chloroform, and ether (= *a.c.e.* mixture) was given at intervals by inhalation; with Cats, chloroform was first given, then the *a.c.e.* mixture, usually in addition about 2 c.c. of 2 p.c. morphia acetate were injected sub-cutaneously; with Rabbits, half to one grain of chloral hydrate was given per rectum, and later the *a.c.e.* mixture was inhaled.

When the animal was thoroughly under the influence of the anæsthetics, the spinal cord was laid bare for a varying distance; as a rule, two or three nerves were first exposed and stimulated, and then progressively the nerves above and below these were exposed and stimulated. The procedure adopted before stimulating the spinal nerve was varied in different experiments; sometimes the nerves just outside the dura mater were tied and cut, and small pieces of sponge were stuffed between the spinal cord and the bone on either side of the cut nerve; occasionally, in addition, the cord was cut at the highest level exposed; sometimes the nerves were tied outside the dura mater, and the spinal cord with its dura mater removed; or the cord was cut into segments corresponding to each spinal nerve; or, lastly the dura mater was opened, the spinal cord removed, and the nerves stimulated outside the dura mater.

I have not observed any constant difference in result to accompany the different methods of procedure, but possibly it is better not to cut the cord when vascular changes are to be observed.

Previous observers do not, as far as I know, mention any difficulty in the exposure of the Ist. thoracic nerve in Rabbits. In my experiments death followed soon, or at once, on cutting through the arches of the last cervical and first two thoracic vertebræ; the large branches of the intervertebral veins which are thus severed, allow air to pass to the heart and the heart stops beating. In one Dog, death was similarly caused. Death, however, does not prevent the effect of the spinal nerves being tested; for, as BUDGE found, the action of these nerves continues for fifteen to thirty minutes after death; but I think that negative results obtained more than five minutes after death are open to suspicion. Death can be avoided by ligaturing the intervertebral veins in the chest, before opening the spinal canal. I have not found a lethal effect to follow section of the vertebral arches below the 2nd thoracic vertebra, except in one case; in this, the arches of five of the mid-thoracic vertebræ were cut through in rapid succession with the result that the heart stopped almost instantaneously.

In stimulating the nerves, a DU BOIS-REYMOND induction coil was used; the primary circuit being arranged for an interrupted current, without HELMHOLTZ side wire, and the electrodes being connected with the secondary circuit. In most of the experiments, currents varying from weak to strong were used, but the results to be described were all obtained, unless otherwise mentioned, by currents barely felt on the tip of the tongue.

In every experiment, as many as feasible of the actions of each spinal nerve were noted, so that the experiments mentioned in dealing with any one class of nerve fibres served to a greater or less extent to determine the origin of other classes of nerve fibres; how far this was done may easily be made out by noting the numbers assigned to the animals in the different Tables.

THE PUPIL, EYELIDS, AND NICTITATING MEMBRANE.

The earliest observations on the origin of the pupillo-dilator fibres from the spinal cord are those of BUDGE and WALLER,* in 1851. Their experiments were made upon Rabbits; the spinal cord was removed from the lower cervical and upper thoracic regions, and the nerves stimulated in their course through the dura mater. They found dilation of the pupil on stimulation of the IInd. thoracic nerve, and not on stimulation of any other spinal nerve. In the following year BUDGE† found that in the Rabbit pupillo-dilator fibres were present, in the Ist. as well as in the IInd. thoracic nerve.

* BUDGE and WALLER, 'Comptes Rendus,' vol. 33, p. 370, 1851.

† BUDGE, 'Comptes Rendus,' vol. 35, p. 255, 1852, and 'Arch. f. physiol. Heilkunde,' 1852, p. 773.

Later (1855) BUDGE* stated that, in addition to the Ist. and IInd. thoracic nerves, the VIth., VIIth., VIIIth., cervical nerves contained dilator fibres for the pupil. The experiments were of two kinds—(1) the spinal cord was removed from the 5th cervical to the 3rd thoracic vertebræ, and the electrodes were placed in the intervertebral foramina; the VIth., VIIth., and VIIIth. cervical, and the first two thoracic nerves were found to cause dilation of the pupil. In experiments conducted in this manner, there must be escape of current, and very little confidence can be placed in the results. (2) The nerve roots were stimulated. In this case, the VIIth. and VIIIth. cervical, and the first two thoracic nerves were found to contain pupillo-dilator fibres. But as the roots were not ligatured, here also there may be some suspicion of an escape of current. It is clear, from the introductory remarks, that some part or other of the experiments not infrequently failed, and the matter is spoken of in such a way as to lead me to think that no especial attention was given to determining the exact origin of the dilator fibres.

In 1862 CLAUDE BERNARD† published the result of his investigations on the spinal origin of the sympathetic fibres, causing dilation of the pupil, opening of the eyelids, protrusion of the eyeball, and retraction of the nictitating membrane. His experiments were made on the Dog. He found that these fibres issued from the spinal cord in the Ist. and IInd. thoracic nerve, and rarely in the IIIrd. thoracic nerve also. He did not find any constant difference in the extent of the dilation produced by the first two thoracic nerves.

SALKOWSKI‡ (1867) made experiments on Rabbits. He cut the roots of the VIIth. and VIIIth. cervical, and of the Ist. and IInd. thoracic nerves, and observed a slight constriction of the pupil, which was not increased by section of the cervical sympathetic; he concluded that the pupillo-dilator fibres issued by these spinal nerves, and by no other. But as he only made one experiment on the effect of cutting the VIIth. and VIIIth. cervical nerves, apart from the section of the first two thoracic, and in that case no change occurred in the pupil, his experiments are inconclusive as to the exact origin of the pupillo-dilator fibres.

FRANÇOIS-FRANCK§ (1878) observed the effect of cutting and of stimulating the *rami* of the lower cervical and first six thoracic nerves in Cats. He states that dilator fibres occur in the rami of the Vth., VIth., VIIth., and VIIIth. cervical nerves; in the rami of the first five thoracic nerves; and occasionally in the ramus of the VIth. thoracic nerve. It is not clear that in these experiments due care was taken to avoid an escape of current.

FERRIER and YEO|| (1881) state that in one experiment on an Ape, no dilation of the

* BUDGE, 'Ueber die Bewegung der Iris.' Braunschweig, 1855, p. 111.

† CL. BERNARD, 'Journ. de la Physiol. de l'Homme et des Animaux,' vol. 5, p. 383, 1862

‡ SALKOWSKI, 'Zeitsch. f. rat. Med.,' vol. 29, p. 167, 1867.

§ FRANÇOIS-FRANCK, 'Travaux du Laboratoire de M. MAREY,' vol. 4, p. 26, 1880.

|| FERRIER and YEO, 'Roy. Soc. Proc.,' vol. 32, p. 12, 1881.

pupil was produced by stimulating the IVth. cervical to the Ist. thoracic nerve, inclusive, but this experiment must be neglected, since, subsequently, FERRIER (1883) pointed out that the nerves taken were really the Vth. cervical to the IInd. thoracic, and that the IInd. thoracic does cause dilation of the pupil.

FERRIER* (1883) gives an account of two experiments on an Ape. He found dilation of the pupil on stimulating the IInd. thoracic, but not on stimulating any other spinal nerve. No great weight can be placed upon the *negative* results obtained by FERRIER, for it is possible that the stimuli employed by him were too weak; his experiments may be taken as showing that the IInd. thoracic is the chief dilator nerve in the Ape. Knowing that Dr. SHERRINGTON was making some observations upon the Ape's spinal nerves, I wrote to him about the origin of the dilators for the pupil; he informed me that he had obtained dilation from the IInd. and the IIIrd. thoracic nerves—more pronounced from the former than the latter—but had not noticed any distinct effect from the Ist. thoracic nerve. Since then, however, he has obtained a distinct, though feeble, dilation from the Ist. thoracic also. The origin of the pupillo-dilator nerves in the Ape, appears (*cp.* p. 94) to be almost identical with their origin in the Rabbit.

Lastly, NAVROCKI and PRZYBYLSKI† find in the Cat that dilation of the pupil is caused by stimulating the VIIIth. cervical and the Ist. and IInd. thoracic nerves in the spinal canal, by stimulating the rami communicantes of VIIIth. cervical and of the Ist. thoracic nerves, and sometimes also by stimulating the ramus of the IInd. thoracic nerve. I am inclined to think—in view of the experiments I mention below—that NAVROCKI and PRZYBYLSKI have fallen into the not uncommon mistake of counting the Ist. thoracic as the VIIIth. cervical nerve.

The chief points in the earlier accounts may conveniently be arranged in the following tabular form.

* FERRIER, 'Roy. Soc. Proc.,' vol. 35, p. 229, 1883.

† NAVROCKI and PRZYBYLSKI, 'Arch f. d. ges. Physiol.,' vol. 50, p. 262, 1891.

PREVIOUS Observation on the Origin of the Oculo-Pupillary Fibres from the Spinal Cord.

	BUDGE and WALLER. 1851.	BUDGE. 1852.	BUDGE. 1855.	BERNARD. 1862.	SALKOWSKI. 1867.	FRANÇOIS-FRANCK. 1878.	FERRIER. 1883.	NAVROCKI and PRZYBYLSKI. 1890.
Animal observed =	Rabbit.	Rabbit.	Rabbit.	Dog.	Rabbit.	Cat.	Ape.	Cat.
Spinal nerves. VI. C. VII. C. VIII. C.	 0 0 0	 0 0 0	 Dilation pupil Dilation pupil Dilation pupil	 0 0 0	 — Section of the roots of these nerves in the spinal canal causes constriction of the pupil (VII. C. to II. Th.)	 Dilation pupil Dilation pupil Dilation pupil	 0 0 0	 0 0 Dilation pupil
I. Th.	0	Dilation pupil	Dilation pupil	Dilation pupil Retraction nict. memb. Opening eye		Dilation pupil	0	Dilation pupil
II. Th.	Dilation pupil	Dilation pupil	Dilation pupil	Dilation pupil Retraction nict. memb. Opening eye		Dilation pupil	Dilation pupil	Dilation pupil
III. Th.	0	0	0	Occasionally slight dilation, &c.	—	Dilation pupil	0	0
IV. Th. V. Th. VI. Th.	0 0 0	0 0 0	0 0 0	0 0 0	— — —	Dilation pupil Dilation pupil Occasionally dilation pupil	0 0 0	0 0 —
Remarks	Spinal cord removed, roots running through the dura mater stimulated	Method like previous	*Cf.* text p. 88.	Nerves in spinal canal stimulated	*Cf.* p. 88.	Results obtained by stimulating the rami communicantes	Nerves stimulated in spinal canal	Nerves stimulated in spinal canal

As I have said above, the induction shocks used as stimuli were, as a rule, in my experiments, just felt on the tip of the tongue; in connection with this it is worth while recalling that BUDGE (*op. cit.*, 1855, p. 80) noticed in the Rabbit that the minimal tetanizing shocks required to produce a dilation of the pupil by stimulation of the sympathetic were stronger than the minimal tetanizing shocks required to give rise to muscular contraction by stimulating the brachial plexus. Similarly, BERNARD (1862) and, later, FERRIER (1883) noticed on stimulating the thoracic nerve roots on the Dog and Ape respectively that contraction of the skeletal muscles was obtained with shocks too weak to cause dilation of the pupil.

The following table gives the results I have obtained on the Cat:—

EFFECT on Pupil, Nictitating Membrane, and Eyelids of Stimulating Spinal Nerves in Cat.

		(1.)	(2.)	(3.)	(4.)	(5.)	(6.)	(7.)	(8.)	(9.)
VI. C.	Pupil Nict. memb. Eyelids	—	—	—	—	—	—	—	—	0
VII. C.	Pupil Nict. memb. Eyelids	0	—	—	0	—	—	—	—	0
VIII. C.	Pupil Nict. memb. Eyelids	0	—	0	0	0	0	0	—	0
I. Th.	Pupil Nict. memb. Eyelids	Good.	—	Good. Less than II. Th.	Good, > II. Th. Good, < II. Th.	Good. Good, < II. Moderate.	Good, > II. Th. Moderate. Moderate, < n.m.	Good, > II. Th. Good, < II. Th.	Good, ? < II. Th. Good.	Good. Good, < II.
II. Th.	Pupil Nict. memb. Eyelids	Good.	—	Good.	Good.	Good.	Good.	Good.	Good.	Good.
III. Th.	Pupil Nict. memb. Eyelids	Slight. Moderate.	Very slight. Moderate.	? 0 Moderate.	Slight. Moderate.	Very slight. Good, < I.	? Slight. Slight to moderate.	Moderate. Good, < II.	Slight. Moderate to good.	—
IV. Th.	Pupil Nict. memb. Eyelids	0 Slight.	0 Slight. Very slight.	0 ? 0	0 Slight.	0 Slight.	0 Very slight.	0 Slight.	0 Slight.	— —
V. Th.	Pupil Nict. memb. Eyelids	0 Very slight.	0	0	0 ? Very slight.	0 ? 0	0	0 Slight, < IV. Th.	0	—
VI. Th.	Pupil Nict. memb. Eyelids	0	0	0	—	—	0	0	0	—
Remarks.		I. Th. lowest nerve causing movement of foot.		I. Th. lowest nerve causing movement of foot.	Both sides stimulated. I. Th. lowest nerve causing movement of foot.	I. Th. lowest nerve causing movement of foot.	I. Th. lowest nerve causing movement of foot.	Both sides stimulated. II. Th. lowest nerve causing movement of foot.	Both sides stimulated. II. Th. lowest nerve causing movement of foot.	I. Th. lowest nerve causing movement of foot.

In this Table—

—, indicates that the nerve was not stimulated.
0, indicates that the nerve was stimulated, and produced no effect.
? 0, indicates that it was not quite certain that on stimulation there was always a complete absence of effect.
Slight, indicates that on stimulation a slight effect was occasionally observed, but it was not certain that the effect was due to the stimulation.

In most of the experiments given above, the various nerves were stimulated over and over again, to compare or make certain of their action. In the case of the nerves which have but a slight action, there are some obvious precautions to take. It is well known that after long or repeated stimulation of the cervical sympathetic, the pupil but slowly regains its normal size, and there is a similar protracted positive after-action on the nictitating membrane and eyelids. Hence it is advisable to stimulate the nerves which have a weak action before those which have a strong action, or, before stimulating the former, to leave an interval of five to ten minutes. Further, in looking for a slight movement of the eyelids, it is advisable to close them before the nerve stimulation; thus a distinct movement of the eyelids may be observed at times when, with widely separated eyelids, no movement is appreciable.

It will be noticed that a nerve, the maximum effect of which is not great in any animal, produced in some animals no effect. The absence of effect might be due either to (1) the absence of the kind of nerve-fibre governing the action in question, or (2) to a few nerve-fibres only being present, the number of these being insufficient in the conditions of the experiment to produce an observable effect.

With regard to (1) there is certainly a variation in different animals in the constitution of the corresponding spinal nerve. This I have shown in the case of the lumbar and upper sacral nerves; it is manifested also in the lower cervical and upper thoracic nerves by the different muscular effects produced by stimulating the corresponding nerves in different animals; thus, out of eight of the experiments mentioned above, the IInd. thoracic nerve in two cases only caused a movement of the foot.

With regard to (2) the case is, I think, equally clear; a nerve which, in favourable conditions, produces a slight but perfectly distinct effect may, later in the experiment or after several stimulations, produce none that can be observed, although its chief action on some other tissue remains obvious throughout.

My experiments are not sufficient to allow me to decide in all cases to which of these causes an absence of effect noted in a particular case is due. I have, however, given my opinion on the matter, in the diagrams of the origin of the different classes of sympathetic fibres in Plates 9 and 10.

On account of the general similarity existing between the Dog and the Cat, I have not thought it worth while to make more than three experiments upon the Dog. In all of these the Ist. and IInd. thoracic nerves produced great dilation of the pupil, and the other customary effects on the eye were equally marked. The IIIrd. thoracic nerve caused in two cases a slight dilation of the pupil, and in one case no certain effect, though there may sometimes have been a trifling dilation; in all cases it caused a slight but distinct movement of the eyelids and nictitating membrane. The IVth. and Vth. nerve in no case had any perceptible result.

On the Rabbit I have made six experiments. Some were made after death (*cf.* Table, p. 94); in these the IInd. thoracic nerve retained its dilator action on the pupil longer than the IIIrd. or the Ist. thoracic nerve, and the effect of the nerves on

the skeletal muscles ceased before that on the pupil and eye. On the other hand, when the upper thoracic nerves were exposed after protracted observation on the lower ones, and death was caused thereby, the effect of the nerves on the eye failed earlier than their effect on the skeletal muscles.

ORIGIN of Oculo-Pupillary Fibres in Rabbit.

	(1.)	(2.)	(3.)	(5.)	(6.)	(7.)
VII. C.	—	—	—	No effect pupil or eye	—	—
VIII. C.	No effect pupil or eye	No effect pupil or eye	—	No effect pupil or eye	No effect pupil or eye	No effect pupil or eye
I. Th.	Moderate dilation pupil Eye opens slightly	Slight dilation of pupil	Slight dilation of pupil	Very slight dilation of pupil	Slow moderate dilation, less than III.	Dilation of pupil Opening of eye
II. Th.	Good dilation pupil Eye opens widely	—	Moderate dilation of pupil	Good dilation pupil	Good dilation	Dilation of pupil Opening of eye
III. Th.	Slight dilation pupil Slight opening eye	—	—	Moderate dilation of pupil	Moderate dilation	Dilation of pupil Opening of eye
IV. Th.	—	—	—	No effect pupil or eye	No effect pupil	—
Remarks.	After death; nerves stimulated in succession from above downward The III. Th. was thus the last stimulated, and hence probably its slight effect The II. Th. was not observed to cause any movement in the foot	After death	After death The II. Th. caused a very slight bending of the foot	The II., III., and IV. nerves were stimulated before death; death was caused by cutting the arches of the lower cervical and upper thoracic vertebræ The II. Th. caused the foot to be bent. Nerves on both sides stimulated	Intervertebral veins ligatured in chest The II. Th. caused the toes to be bent	Intervertebral veins ligatured in chest The dilation of the pupil was slow with all three thoracic nerves, but was quicker with the II. than with the other two The II. Th. caused the foot to be bent

The results of the experiments are:—

1. The lower cervical nerves in no instance give the faintest indication of action upon either the pupil, the nictitating membrane, or the eyelid.

The VIIIth. cervical nerve—the one which most frequently has been said to contain pupillo-dilator fibres—I have stimulated with currents of varying strength and of varying duration, without ever producing any effect upon the pupil or eye. In the experiment given below (Exp. I.), stimulation of the Ist. and IInd. thoracic nerves caused a considerable, though slow, dilation of the pupil when the index of the secondary coil of the induction machine was at 15 centims. of the scale, and a rapid complete dilation with all greater strengths of current, whilst stimulation of the VIIIth. cervical nerve was without a trace of effect on the pupil, whether the index of the secondary coil was at 15 centims., or at 0, or at any intermediate position.

Experiment I.

Cat (9). Chloroform; 2 c.c. 2 p.c. morphium acetate injected subcutaneously; at intervals *a.c.e.* mixture given.

Expose the spinal cord in the lower cervical and upper thoracic region, cut through the cord between the VIth. and VIIth. cervical spinal nerves, lift up the lower piece of cord by its dura mater, tie and cut just outside the dura mater the VIIth. and VIIIth. cervical, the Ist. and IInd. thoracic nerves, remove the cord down to the 3rd thoracic vertebra.

The pupil is of medium size, the nictitating membrane is protruded over the eye, the ear is pale.

The nerves on the right side only were stimulated; when the index of the secondary coil is at 8 centims. of the scale, and the electrodes are placed on the tip of the tongue, the induced currents are feebly felt. Below s.c. is used for the index of the secondary coil.

12.40. Stim. VII. C.; s.c. at 8; strong contraction of shoulder and leg, slight contraction of foot, claws not protruded.

No effect on pupil, nictitating membrane, eyelids, eye, vessels of ear, or sweat glands of fore-foot.

12.43. Stim. VII. C.; s.c. at 7; stronger tetanus of muscles of leg, otherwise result the same.

12.45. Stim. VII. C.; s.c. at 6; same result.

12.47. Stim. VII. C.; s.c. at 4; same result.

12.49. Stim. VIII. C.; s.c. at 8; strong contraction shoulder, leg, and foot; foot bent, claws protruded, toes separated.

No effect on pupil, nictitating membrane, eyelids, eye, vessels of ear, or sweat glands of fore-foot.

12.52. Stim. VIII. C.; s.c. at 7; same result.

12.54. Stim. VIII. C.; s.c. at 6; same result.

12.56. Stim. VIII. C.; s.c. at 4; same result.

1.0. Stim. I. Th.; s.c. at 8; foot bent, claws protruded, toes separated.

Pupil dilates apparently to its full extent, eye protrudes, eyelids widely separated, nictitating membrane withdrawn.

Distinct, though slight, contraction of vessels of ear, no effect sweat glands of fore-foot.

1.4. Stim. I. Th.; s.c. at 8; same result.

1.8. Stim. II. Th.; s.c. at 8; no effect on leg or foot.
Pupil dilates apparently to its full extent, effect on eye and eyelids rather greater than with I. Th., nictitating membrane withdrawn, ear rapidly becomes pale.

Open the mouth widely and note the colour of the palate and of the rest of the mucous membrane of the mouth.

1.12. Stim. II. Th.; s.c. at 8; very obvious contraction of palatine artery, marked pallor of whole of mucous membrane of right side of mouth, moderate pallor of right side of tongue, and slight on left side.

1.16. Stim. I. Th.; s.c. at 6; slight pallor of mouth and ear; other effects not looked for.

1.20. Stim. I. Th.; s.c. at 4; same result.

2.0. Stim. I. Th.; s.c. at 4; slight pallor mouth and ear, good dilation pupil, other eye effects also good.

2.5. Stim. II. Th.; s.c. at 4; great pallor mouth and ear, good dilation pupil, other eye effects also good.

2.8. Stim. VIII. C.; s.c. at 15; weakish contraction shoulder and leg, no effect on pupil, eye, bloodvessels, or sweat.

2.11. Stim. VIII. C.; s.c. at 0; for 60 secs., usual contraction in leg, no effect on pupil, eye, bloodvessels, or sweat.

2.14. Stim. I. Th.; s.c. at 15; slow action on pupil and eye.

2.16. Stim. II. Th.; s.c. at 15; slow dilation pupil, fairly rapid withdrawal of nictitating membrane.

Tie and cut VIth. cervical nerves; stimulation of the right VIth. cervical nerve (s.c. at 8 and s.c. at 0) causes contraction muscles of shoulders and leg, but has no effect on the pupil, the eye, the vessels of mouth and ear, or on the sweat glands of the fore-foot.

2. The pupil receives dilator fibres from the Ist., IInd., and IIIrd. thoracic nerves. The relative effect of these nerves varies somewhat in different animals of the same species, and varies considerably in animals of different species.

In the Cat and Dog both the Ist. and IInd. thoracic nerves cause great dilation of the pupil; in the Cat, as a rule, the Ist. produces greater dilation than the IInd. thoracic, but this is not always the case, and sometimes the IInd. is more powerful than the Ist. thoracic nerve. The IIIrd. thoracic nerve has a comparatively slight action, and the extent of its action varies; in some cases the dilation produced by it is readily observed, in others it requires special attention.

I had thought that, perhaps, the IIIrd. thoracic nerve might produce a greater effect if the pupil were contracted. To produce contraction, I injected a few milligrms. of pilocarpin. The effect of this, however, was not an increase but a decrease of the dilator action of the nerve.

Experiment (3) on the Cat, in which I did not observe a distinct dilation of the pupil, on stimulating the IIIrd. thoracic nerve, was one chiefly directed to other ends, and the eye effects were only observed incidentally.

In the Rabbit, the IInd. thoracic nerve is the chief dilator nerve for the pupil; the IIIrd. thoracic nerve produces a considerable dilation, but less promptly than the

IInd.; the Ist. thoracic has the least action of the three, and in some cases has a very slight effect.

3. No dilation of the pupil is caused by stimulating any spinal nerve below the IIIrd. thoracic. In view, however, of the action of the IVth. thoracic upon the nictitating membrane and eyelids in the Cat, it is possible that, in some cases and in favourable circumstances, a slight dilation of the pupil might be observed on stimulation of the IVth. thoracic nerve.

4. The nerve-fibres causing retraction of the nictitating membrane and opening of the eyelids, have in the Cat a more extended origin than the dilator fibres for the pupil. They arise from the first four thoracic nerves, and sometimes from the fifth also. In nearly all cases the IInd. thoracic nerve is the most effective; the Ist. thoracic is more effective than the IIIrd., the IVth. has a slight effect, and may sometimes be easily overlooked; the Vth. causes at best but a trifling movement.

It will be seen that my results on the Dog confirm the results of CL. BERNARD, with the exception of the rarity of action of the IIIrd. thoracic, and it is possible that on this point my cases may have been exceptional. In the Cat and Rabbit, my results are on many points not in agreement with those of previous observers.

ORIGIN OF THE VASO-MOTOR FIBRES FOR THE HEAD.

BUDGE* (1853), following the lines of BERNARD's description of the effects of section of the cervical sympathetic, stated that the fibres, section of which causes an increase of temperature in the head, pass from the spinal cord in the VIIIth. cervical and first two thoracic nerves. His experiments consisted in removing the spinal cord from the 8th cervical to the 2nd thoracic vertebræ inclusive, and in cutting the issuing nerves. He does not, however, mention any experiment on the effect of cutting one of these nerves apart from the other two, or on the effect of stimulating them, so that he can hardly be considered to have shown more than that fibres, later known as vaso-motor, issue by one of the three nerves.

BERNARD† (1862) came to the conclusion that in Dogs vaso-motor nerves for the head were absent from the Ist. and IInd. thoracic nerves, since section on one side of these nerves in the spinal canal caused no, or only a slight and temporary, increase of temperature on that side of the head. But he found a considerable rise of temperature when the sympathetic was cut between the 2nd and 3rd ribs; whether the nerve-fibres producing this effect arise from the spinal cord or from the sympathetic ganglia, BERNARD left undecided.

SALKOWSKI‡ (1867) states that in Rabbits the vaso-motor fibres for the ear arise from the VIIth. and VIIIth. cervical and the Ist. and IInd. thoracic nerves. After

* BUDGE, 'Comptes Rendus,' vol. 36, p. 377, 1853.

† BERNARD, 'Comptes Rendus,' vol. 55, p. 381, 1862.

‡ SALKOWSKI, 'Zeitschrift. f. rat. Medicin,' vol. 29, p. 167, 1867.

cutting these nerves in the spinal canal, he found a dilation of the vessels of the ear. He gives no experiment upon the effect of cutting the cervical nerves by themselves, and one only on the effect of cutting them after the first two thoracic nerves had been severed; in the latter case the vessels of the corresponding ear dilated strongly, and underwent, on section of the cervical sympathetic, no further dilation. The experiment is inconclusive, since the dilation on section of the cervical nerves may have been a reflex one, and section of the cervical sympathetic would probably have no effect on strongly dilated vessels; sometimes, indeed, it has very little effect when the vessels are not dilated.

DASTRE and MORAT* (1883) state that the vaso-dilator fibres for the ear and other parts of the head leave the cord by the last cervical and first two thoracic nerves, and the vaso-constrictor fibres for the same region leave the cord by the IIIrd., IVth., and Vth. thoracic nerves.

DASTRE and MORAT† find, however, that the vaso-dilator fibres for the bucco-facial region of the Dog issue by the IInd., IIIrd., IVth., and Vth. thoracic nerves. On various grounds they conclude that vaso-constrictor fibres accompany the vaso-dilators.

I append a Table giving a summary of these observations.

* DASTRE and MORAT, 'Comptes Rendus,' Feb. 12, 1883.

† DASTRE and MORAT, 'Système Nerveux Vaso-moteur.' Paris, 1884, p. 132.

PREVIOUS Observations on the Origin of Vaso-motor Fibres for the Head.

	BUDGE, 1853.	BERNARD, 1862.	SALKOWSKI, 1867.	DASTRE and MORAT, 1883.	DASTRE and MORAT, 1884.
	Rabbit.	Dog.	Rabbit.	On vessels of ear.	On bucco-facial region of Dog.
VII. C.	—	—	Vaso-constrictor		
VIII. C.	Vaso-constrictor . . .	—	Vaso-constrictor . . .	Vaso-dilator	
I. Th.	Vaso-constrictor . . .	0	Vaso-constrictor . . .	Vaso-dilator	
II. Th.	Vaso-constrictor . . .	0	Vaso-constrictor . . .	Vaso-dilator	Vaso-dilator
III. Th.	—	Section of sympathetic below ganglion stellatum caused rise of temperature on same side of head. Origin of the fibres not followed	—	Vaso-constrictor . . .	Vaso-dilator
IV. Th.	—	—	—	Vaso-constrictor . . .	Vaso-dilator
V. Th.	—	—	—	Vaso-constrictor . . .	Vaso-dilator
Remarks	Nerves in spinal canal cut, increase in temperature in ear (and ? rest of corresponding side of head) noticed	Nerves in spinal canal cut, and increase in temperature on same side looked for	Nerves in spinal canal cut, and subsequently cervical sympathetic. Temperature of same side of head noted	Nerves in spinal canal, or rami communicantes stimulated	Nerves in spinal canal stimulated

The regions of the head which I have observed for pallor or flushing as the result of stimulating the spinal nerves are, in the Cat, the ear, the mucous membrane of the mouth and lips, and the tongue; in the Dog, the same parts, with the omission of the ear, and the addition of the conjunctiva; in the Rabbit I have observed the ear, conjunctiva, and gums. These parts do not all show vascular effects with equal distinctness; in the Rabbit it is well known that the ear is the best part for direct observation; in the Cat the ear is also good, though sometimes the contraction of the palatine artery is more striking than that of the auricular artery. In the one experiment made on the Dog the mucous membrane of the floor of the mouth was found to respond more distinctly than any other part.

In addition to these direct observations I have made one indirect observation on the origin of the vaso-constrictor fibres of the sub-maxillary gland. A little pilocarpin produces, as is known, a protracted and regular secretion of saliva; if the cervical sympathetic be stimulated whilst this secretion is going on, there is after a normal transient increase, a decrease in the rate of secretion; this is accompanied by a constriction of the blood-vessels of the gland. In the absence, then, of any evidence of inhibitory secretory fibres in the sympathetic, and in view of HEIDENHAIN's experiment on decreasing the blood-flow to the gland by compressing the artery, we may take a decrease in the rate of the pilocarpin-secretion produced by stimulating a spinal nerve as showing the presence of vaso-motor fibres in the nerve. The result of the experiment made in this way is given in the Table below [Dog (3)]. Some further account of the experiment will be found in the section dealing with the secretory nerves.

My experiments have not been directed to determining with accuracy any differences which there may be in the origin of the vascular nerves of the different parts of the head. They show, however, that if there are differences, the differences are not great.

The origin of the vascular nerve-fibres in the Rabbit has certain peculiarities which make it desirable to treat it by itself.

ORIGIN in the Cat and Dog of Vaso-Motor Fibres for the Head.

	Cat (6).	Cat (8).	Cat (9).	Cat (10).	Dog (2).	Dog (3).
VI. C.	—	—	0	—	—	—
VII. C.	—	—	0	—	—	—
VIII. C.	0	—	0	—	0	—
I. Th.	Slow pallor ear . .	r. ? 0 l. 0	Slight pallor ear and muc. memb. mouth	—	Pallor	Constriction vessels sub-max. gland
II. Th.	Complete pallor ear	r. Complete pallor ear l. Complete pallor ear	Complete pallor ear and muc. memb. mouth	—	Pallor < I. . . .	Constriction vessels sub-max. gland
III. Th.	Complete pallor ear	r. Complete pallor ear l. Complete pallor ear	—	Complete pallor ear and slight of muc. mem. mouth	Slight pallor . . .	Constriction vessels s.m. gland and pallor mouth
IV. Th.	Complete pallor ear < II. or III.	r. Pallor ear, < II. or III. l. Complete pallor ear	—	Complete pallor ear and very slight of mouth	? Slight pallor . .	Slight constriction vessels s.m. gland and pallor mouth
V. Th.	Pallor ear, not complete	r. Slow pallor ear . l. Complete pallor ear	—	Rather slow pallor ear; none seen in mouth	0	No certain effect
VI. Th.	0	r. and l. 0	—	0	0	—
VII. Th.	—	0	—	0	—	—
Remarks	Cord not cut. Section of I. to IV. caused flushing of the ear	Cord in region removed. Ear pale. The two sides are indicated by r. and l.	Cord in region removed. Ear pale. This is from Exp. 1 given on p. 95.	Cord not cut. Nerves tied and cut from below upwards. After cutting IV. and III. ear flushed	Cord not cut. Parts observed were muc. memb. mouth, lips, conjunctiva	Cord not cut. For method of determining action in sub-max. gland, *cf.* p. 106.

The results of these experiments are:—

1. The VIth., VIIth., VIIIth. cervical nerves cause neither contraction nor dilation of the vessels of the head.

2. The Ist. thoracic nerve has a slight and inconstant effect in the Cat; the effect is apparently greater in the Dog. In Cats, it may be distinct enough to be beyond question, or it may not be perceptible in the conditions of the experiment.

3. The IInd. and IIIrd. thoracic nerves cause complete and rapid constriction of the small arteries. In the Cat the IIIrd. nerve has seemed to me to produce constriction rather more quickly than the IInd.

4. The IVth. thoracic also causes complete constriction, but more slowly than either the IInd. or IIIrd.; in the Dog its effect is less than in the Cat.

5. The Vth. thoracic nerve has less effect than the IVth.; in the Cat the constriction caused by it, though it may be complete, is usually slow.

In Cat (8), however, stimulation of the left Vth. thoracic for three seconds, with induction shocks of moderate strength, was sufficient to cause complete constriction of the auricular artery lasting for half to one minute.

In the Dog I have no satisfactory evidence of the existence of vaso-motor fibres in the Vth. nerve, but I think it probable that they are sparsely present.

6. The thoracic nerves below the Vth. have not in the Cat and Dog any effect upon the vessels of the head.

It has already been mentioned that DASTRE and MORAT found in the Dog flushing of the bucco-facial region on stimulating any one of the IInd. to Vth. thoracic nerves. In my experiments no flushing was observed, although shocks of widely different strength were used; the nerves which produced any effect, viz., the Ist. to IVth., caused pallor only in this region. At the same time I have no doubt that, by varying the experimental conditions, flushing, instead of pallor, would be obtained.

Turning now to the Rabbit, we have—

ORIGIN in the Rabbit of the Vaso-motor Fibres for the Head.

	(4.)	(5.)	(6.)	(7.)
VIII. C.	—	—	0	0
I. Th.	—	—	? 0	0
II. Th.	—	Slight constriction of artery of ear.	Slight slow constriction of artery of ear, chiefly lower half.	Complete, but slow, constriction of artery of ear.
III. Th.	—	Complete, but slow, constriction of artery of ear. Conjunctiva paler.	Complete, but slow, constriction of artery of ear.	Complete, but rather slow, constriction of artery of ear; more in lower than upper half, most in mid portion. Conjunctiva paler; effect was very marked.
IV. Th.	Complete constriction of artery of ear.	Complete constriction of artery of ear. Conjunctiva and gums paler.	Complete constriction of artery of ear.	—
V. Th.	Complete constriction of artery of ear.	Complete constriction of artery of ear. Conjunctiva and gums slightly pale.	Complete constriction of artery of ear.	—
VI. Th.	Complete constriction of artery of ear, rather more slowly than with IV. or V.	Complete, but rather slow, constriction of artery of ear.	Complete constriction of artery of ear.	—
VII. Th.	Complete constriction of artery of ear, rather more slowly than with IV. or V.	Complete, but slow, constriction of artery of ear.	Complete constriction of artery of ear.	—
VIII. Th.	Slow constriction of artery of ear, chiefly mid portion. Occasionally there is dilation of artery.	Slow constriction of artery of ear, chiefly mid portion.	Slight constriction of artery of ear in its mid portion.	—
IX. Th.	? 0	? 0	—	—
Remarks .	Nerves exposed from below upwards; the heart stopped on cutting through the upper thoracic vertebræ. Nerves on both sides stimulated.	Nerves exposed from below upwards. Spinal nerves tied and cut ouside dura mater, cord not cut. After stimulation of the VI. to VIII. nerve there is generally a dilation of the artery.	Intervertebral veins tied in thorax, before exposing the spinal cord. Spinal nerves tied and cut outside dura mater; cord not cut until upper four nerves had been stimulated. Nerves on both sides stimulated.	Intervertebral veins tied in thorax, before exposing the spinal cord. Spinal nerves tied and cut outside dura mater, cord not cut.

Comparing the Rabbit with the Cat and Dog, we see that :—

1. The upper limit of origin of the vaso-motor nerves for the head is rather lower in the Rabbit; for in this animal the Ist. thoracic apparently sends no vaso-motor fibres to the sympathetic, and the IInd. comparatively few.

2. In the Rabbit the origin of the sympathetic vaso-motor nerve-fibres is more extended than in the Cat and Dog, for in the former they originate from seven spinal nerves (IInd. to VIIIth. thoracic). There are other and minor differences which need not be detailed here.

It is noticeable that the uppermost and the lowermost nerve, each producing but a slight effect upon the ear, produces a local effect; the middle portion of the artery, or the mid together with the lower portion becoming completely constricted, whilst the rest shows little or no change.

When a nerve has a slight effect only, its effect is usually variable; it may cause a brief constriction followed by a pronounced dilation, whilst the nerve is still being stimulated, or a dilation alone; the dilation is more marked with weak than with strong currents.

Secretory Nerves to the Sub-Maxillary Gland.

I do not know of any observations on the exact origin from the spinal cord of the sympathetic secretory fibres to the salivary glands.

I have confined my attention to the sub-maxillary gland of the Cat and Dog. The chordo-lingual nerve (*i.e.*, the lingual nerve before the chorda tympani leaves it) is cut, a cannula tied in the duct, the animal turned over and the spinal nerves laid bare and stimulated. The observation requires some care, since, in the position of the animal, the cannula unless carefully supported, causes by its weight a kink in the duct. I have not found that the spinal nerves, with the exception of the IInd. thoracic, cause a secretion with the same constancy as they cause oculo-pupillary and vascular effects. A longer interval must be left between successive stimuli, or the stimuli, if repeated, must be brief. Generally speaking, it is best to stimulate for ten seconds out of each thirty, during about three minutes. The absence of secretion on stimulation, although the nerve contains secretory fibres, is probably in the main due to the retarding effect on secretion of the diminished blood supply to the gland.

In the Cat, the cervical sympathetic produces normally a fairly rapid secretion for ten to fifteen seconds; I have in no case obtained with any spinal nerve a secretion as plentiful as that given ordinarily by the cervical sympathetic; although as we have already seen, an apparently maximal effect on the pupil and eye can be produced by two spinal nerves, and an apparently maximal effect on the vessels of the ear by three or four spinal nerves.

When a spinal nerve, stimulated with weak induction shocks, fails to cause a secretion, although other visceral effects are produced, the strength of the current

should be progressively increased. It is with secretory fibres only that I have sometimes found it necessary to use currents distinctly strong to the tip of the tongue, in order to produce an effect.

ORIGIN of Secretory Nerves for the Sub-Maxillary Gland of the Cat and Dog.

	Cat.				Dog.		
	(4.)	(5.)	(7.)	(8.)	(1.)	(2.)	(3.)
VII. C.	0	—	—	—	—	—	—
VIII. C.	0	0	0	—	—	0	—
I. Th.	Occasionally trace secretion	0	0	? 0	? Slight	Sometimes slight	Secretion
II. Th.	Good secretion	Good	Good	Moderate	Slight	Moderate	Secretion
III. Th.	Usually a slight secretion	Moderate	Moderate	Sometimes moderate	Sometimes slight	0	Secretion
IV. Th.	0	0	Moderate	? 0	—	0	Slight secretion
V. Th.	0	0	Slight	0	—	0	? Slight secretion
VI. Th.	—	—	0	0	—	—	0
Remarks	—	—	—	—	After death	—	For method and details *cf.* Exp. II., p. 106

It will be seen from the experiments that the IInd. thoracic nerve had a distinctly greater effect on secretion than any other.

The IIIrd. thoracic nerve, in each of the experiments, caused some secretion, but in three of these several stimuli were sometimes necessary before a secretion was visible.

The IVth. and Vth. thoracic nerves gave rise, in one Cat only, to an appreciable secretion; the IVth. nerve was more effective than the Vth.; in the other cases the secretion was a secondary consideration, and it is probable that, with greater precautions, the IVth. and Vth. nerves might have been found to contain a few secretory fibres. In the Dog, though in an experiment conducted by a different method, secretory fibres were found in the IVth nerve; with regard to the Vth. the evidence was not very satisfactory, but apparently a few secretory fibres were present.

The Ist. thoracic nerve in the Cat gave evidence once only of containing secretory fibres; in the Dog, on the other hand, more or less satisfactory evidence was obtained in all three cases.

The origin of the secretory fibres in the Cat and Dog bears, then, a very close resemblance to the origin of the vaso-motor fibres in these animals; in the Dog both

secretory and vaso-motor fibres are more represented in the Ist. thoracic than in the Vth.; whilst the reverse is the case in the Cat.

In order to allow a judgment upon the experiments in the Dog (No. 3), spoken of above as being conducted by a different method, some details regarding it must be given. I have shown* that, ordinarily, whilst a pilocarpin secretion is going on, a brief stimulation of the sympathetic causes an increase in the secretion greater than the amount produced when there is no pilocarpin secretion. From this it seemed probable that if pilocarpin were given, and the spinal nerves stimulated, secretory fibres might be detected, even though present in very scanty numbers. The experiment thus conducted completely answered expectation; I give here sufficient of it to illustrate its chief point.

Experiment II.

Dog (3).—Morphium acetate injected sub-cutaneously; *a.c.e.* given nearly continuously throughout the experiment.

On the right side, cut the chordo-lingual nerve, and tie a cannula in the sub-maxillary duct.

Cut through the arches of the 2nd to the 6th thoracic vertebræ, tie and cut the IIIth., IVth., and Vth. thoracic nerves outside the dura mater.

4.0. Inject 2 mgms. of pilocarpin nitrate into the jugular vein; connect the sub-maxillary cannula with a tube graduated in millimetres, and make some preliminary observations. The rise of the saliva in the tube was read off in millimetres every fifteen seconds. The tube, when full, was emptied, this is indicated by dash —, it occupied fifteen to forty-five seconds. When a number is underlined it means that one of the spinal nerves was stimulated during the secretion of the saliva indicated by the number; the number of the thoracic nerve stimulated is placed under the line.

A few only of the observations are here given.

4.10. Secretion very slow.

4.14. Inject 1·5 mgm. of pilocarpin nitrate into jugular.

21, 21, 21, $\underset{\text{IV.}}{\underline{28,}}$ – 27, 28, 22, $\underset{\text{V.}}{\underline{24, 23,}}$ 19, 21, $\underset{\text{III.}}{\underline{29, 17, 13,}}$ – 35, 38, 30, 29, $\underset{\text{III.}}{\underline{30, 15, 15,}}$ 18,

– pause, 9, 8, 8, $\underset{\text{IV.}}{\underline{31, 6, 4, 8,}}$ 10, 11, 11, 12, 9, 9, $\underset{\text{V.}}{\underline{13, 7, 9,}}$ 9, 12, – 11, 10, 10, $\underset{\text{III.}}{\underline{51,}}$ 8, $\underset{\text{V.}}{\underline{24, 12.}}$

Expose tie and cut IInd. and Ist. thoracic nerve.

6.4. Inject 1·5 mgm. pilocarpin nitrate.

16, 17, 15, $\underset{\text{I.}}{\underline{48, 26, 22,}}$ 30, 33, 26, pause, 24, $\underset{\text{II.}}{\underline{50, 28, 30, 24,}}$ 25, 30, – 25, 23, $\underset{\text{II.}}{\underline{37, 15, 15, 15,}}$

14, 18, 36, pause, 30, 29, $\underset{\text{I.}}{\underline{25, 16, 15, 16,}}$ 22, 24.

The greater part of the increased flow of saliva, following immediately on stimulation, occurred in the first 7 to 10 seconds. Allowing for the slow gradual decrease of the pilocarpin secretion, an increase in rate of flow on or after stimulation implies the presence of secretory nerve fibres, a decrease in the rate of flow implies the presence of vaso-motor fibres. The IInd. thoracic caused a very feeble movement of the toes.

* 'Journal of Physiology,' vol. 10, p. 291, 1889.

Cardiac Accelerator Fibres.

The existence in Mammals of cardiac accelerator fibres passing from the spinal cord through the sympathetic system, was made probable by the experiments of v. Bezold,* shown by those of M. and E. Cyon.† Although many observations have been carried out on the accelerator fibres, very few have been directed to the exact determination of the spinal nerves which contain them. Bever and v. Bezold‡ found in Rabbits that, after the spinal cord had been cut at the level of the second thoracic vertebra, a quickening of the rate of heart-beat could still be obtained without a rise of blood-pressure by stimulating the cervical spinal cord; they thought that spinal cardiac nerves left the cord chiefly, if not entirely, above the second thoracic vertebra. As the result of direct stimulation, they concluded that the accelerator nerve fibres passed to the sympathetic by the radix longa and radix brevis of the ganglion stellatum, that is to say, they issued from the cord by the lower cervical nerves.

Schmiedeberg§ stimulated in the Dog the radix longa and radix brevis, apparently once only, and did not find an accelerating action. He considered, however, that his experiments were not sufficient to prove the absence of accelerating fibres in these roots.

Boehm and Nussbaum|| stimulated the radix longa in the Cat, and in two out of five cases obtained distinct acceleration. The radix longa they describe as coming from the VIth. and VIIth. cervical nerves.

Stricker and Wagner,¶ in one experiment on the Dog, stimulated the upper rami of the ganglion stellatum, and observed no effect in the heart. They obtained, however, acceleration on stimulating the sympathetic below the ganglion stellatum; and they found that, when the sympathetic was tied about the level of the seventh rib, and the rami up to the ganglion stellatum severed, the acceleration was greater the nearer the ganglion the sympathetic was stimulated. These experiments tend to show that the VIth., Vth., IVth., IIIrd., and probably also the IInd., thoracic nerves contain accelerator fibres.

The only observations which I have been able to find, with regard to the effect on the heart of stimulating the spinal nerves in the spinal canal, are some incidentally mentioned by Bradford** in a paper on the renal vaso-motor nerves, and by Bradford and Dean†† in a paper on the pulmonary vaso-motor nerves; in both papers the IInd.

* v. Bezold, 'Unters. ü. d. Innervation des Herzens,' 1863, 1864.

† M. and E. Cyon, 'Archiv f. Anat. u. Physiol.,' p. 389, 1867.

‡ Bever and v. Bezold, 'Unters. a. d. Physiol. Laboratorium in Würzburg,' Part II., p. 235, 1867.

§ Schmiedeberg, 'Ber. ü. d. Verhandl. d. k. Sächs. Gesellsch. zu Leipzig,' 1871, p. 148.

|| Boehm and Nussbaum, 'Arch. f. exp. Pathol. u. Pharmakol.,' vol. 4, p. 255, 1875.

¶ Stricker and Wagner, 'Sitzungsb. d. Wiener Akad.,' vol. 77, Abt. iii., p. 103.

** Bradford, 'Journ. of Physiol.,' vol. 10, p. 358, 1889.

†† Bradford and Dean, 'Roy. Soc. Proc.,' vol. 45, p. 369, 1889.

and IIIrd. thoracic nerves are spoken of as producing acceleration of the heart, and in the latter paper it is implied that the IInd. thoracic has a greater effect than the IIIrd. thoracic nerve.

PREVIOUS Observations on the Origin of Accelerator Fibres from the Spinal Cord.

	BEYER and v. BEZOLD, 1867. Rabbit.	SCHMIEDEBERG, 1871. Dog.	BOEHM and NUSSBAUM, 1875. Cat.	STRICKER and WAGNER, 1878. Dog.	BRADFORD, 1889. BRADFORD and DEAN, 1889. Dog.
VI. C.	Accelerator fibres found in radix longa and in radix brevis.	No accelerator fibres found in radix longa or in radix brevis. Apparently one experiment only.	Accelerator fibres found in radix longa in two out of five experiments.	No accelerator fibres found in upper rami of ganglion stellatum.	
VII. C.					
VIII. C.			..		
I. Th.	..	..	..		
II. Th.	..	..	..	Accelerator fibres found in thoracic sympathetic, number being greater in passing from the 6th ramus upwards to the ganglion stellatum.	Accelerator fibres.
III. Th.	..	..	..		Accelerator fibres.
IV. Th.	..	..	..		
V. Th.	..	..	..		
VI. Th.	..	..	..		

The accelerator nerve I have investigated in the Cat only. In the section treating of the secretory fibres, we have seen that three out of the four nerves which may be regarded as normally containing secretory fibres, may, in a particular animal, produce no secretion on stimulation. I have interpreted this as meaning that there are certain conditions in the experiment which tend to prevent the occurrence of a secretion.

A similar state of things holds, and perhaps even to a still greater degree, in regard to the accelerator nerve-fibres. In one animal, the Ist. to the IVth. thoracic nerves will constantly produce marked quickening of the heart-beat, whilst in another animal, the Ist. to the IVth. thoracic nerves will as constantly be without effect. I take this to be due primarily to varying responsiveness to accelerator impulses—at a certain degree of irresponsiveness each nerve will fail to produce an effect according to the number of accelerator fibres it contains—and secondarily, to a variation in the number of accelerator nerve-fibres in the corresponding nerves.

BOEHM and NUSSBAUM, STRICKER and WAGNER, and others, have noticed that the "accelerator nerves" in the thorax have much less effect on the left side than on the right. This was also the case in my experiments.

ORIGIN of Accelerator Fibres in Cat.

	(4.)	(5.)	(6.)	(7.)
VII. C.	0	—	—	—
VIII. C.	0	0	0	0
I. Th.	0	? Very slight	Moderate or slight	Good
II. Th.	Good	Slight	Moderate	Good; acceleration lasts longer than with other nerves
III. Th.	Moderate	Good	Good	Good
IV. Th.	0	Slight	Moderate	Good
V. Th.	0	? Very slight	Moderate or slight	0
VI. Th.	—	—	? Very slight	0
Remarks. .	Above is of nerves on the right side. On the left side indications, but no satisfactory proof, of accelerator fibres were found in the II. and III.	Nerves on right side only stimulated	Above is of nerves on the right side. No satisfactory evidence of accelerators was obtained on the left. In the experiment the spinal cord was not cut	Above is of nerves on the right side. No satisfactory evidence of accelerators on the nerves tried on the left side (I., II. and VI.), *cf.* details, Experiment III.

I give some details of one of the experiments quoted in the preceding table, in order to show the degree of acceleration obtained, and its independence of the arterial blood-pressure.

Experiment III.

Cat (7). Chloroform, 2 c.c., 2 p.c. morphia injected sub-cutaneously; *a.c.e.* mixture during most of the time. The spinal cord was laid bare from the VIIIth. cervical to the VIth. thoracic nerve, the dura mater cut through and the posterior roots cut, the cord cut above the VIIIth. cervical nerve, turned back, and removed, the anterior roots being cut; the dura mater was then cut into pieces to afford a hold for lifting up the several nerves, which were stimulated outside the dura mater. The blood-pressure was taken by a mercurial manometer connected with the right carotid; chordo-lingual nerve cut, cannula tied in left sub-maxillary duct.

With the aid of two assistants, the effect of stimulating the various spinal nerves on the pupil, eye, saliva, hair, sweat were observed, in addition to that on the blood-pressure and heart-beat recorded on the tracing. In order to avoid obscuring the main point, viz., the effect on the heart, these other observations are omitted, but it is important to remember that in every case of stimulation, whether it caused an acceleration of the heart or not, the full irritability of the nerve was shown by its characteristic action on other tissues.

The duration of the stimuli varied from 5 to 15 secs.; secondary coil at 7 gave shocks weak to the tip of the tongue.

	Nerve stimulated.	Position of index of sec. coil.	Rise of blood-pressure in mm. Hg as result of stimulation.	Number of heart-beats in 10 seconds.	
				Before stimulation.	During or after stimulation.
Right side . .	VI. Th.	7	27	19	18
	VI. Th.	6	28	21	22
	VI. Th.	6	26	23	23
	VI. Th.	5	28	23	23
	The very gradual rise in rate of heart-beat occurred so far as could be seen independently of the stimulation.				
	V. Th.	6	30	23	23
	V. Th.	6	20	23	23
	V. Th.	5	10	23	23
	IV. Th.	6	14	23	29
	IV. Th.	6	10	22	29
	IV. Th.	6	10	21	28
	IV. Th.	6	13	22	29
	II. Th.	6	10	20	32
	II. Th.	6	12	21	32
	II. Th.	6	7	25	31
	III. Th.	6	15	22	30
	III. Th.	6	14	22	30
	III. Th.	6	10	24	29
	VI. Th.	6	20	25	19
	II. Th.	6	8	20	30
	VI. Th.	6	26	23	20
	VI. Th.	6	26	22	22
	VI. Th.	5	21	22	22
	VI. Th.	5	8	22	22
Left side . .	VI. Th.	6	18	22	22
	VI. Th.	6	26	22	22
	VI. Th.	6	25	22	22
	VI. Th.	5	26	22	22
	II. Th.	5	5	22	23
	II. Th.	5	4	22	24
	II. Th.	5	7	20	23
Right side . .	I. Th.	6	5	18	27
	I. Th.	6	6	20	29
	VIII. C.	6	0	18	18
	VIII. C.	6	0	17	17
	I. Th.	6	5	16	25
Left side . .	I. Th.	6	0	16	16
	I. Th.	6	0	16	18
	I. Th.	6	0	16	19
	VI. Th.	6	40	16	19
	VI. Th.	6	36	20	21

Inject 1·3 mgrms. of pilocarpin nitrate into a vein; the heart for a time beats very slowly, but soon recovers a rate of 17 in 10 secs.; stimulate in succession the nerves on the right side and then on the left, not one of them now produces the faintest effect upon the rate of heart-beat.

From the experiments given above I conclude that—

1. The lower cervical nerves contain no cardiac accelerator fibres.

2. The nerve which has the maximum number of accelerator fibres is in some animals the IInd., in others the IIIrd., thoracic nerve.

3. The Ist. to the IVth. thoracic nerves contain in some animals a considerable number of accelerator fibres, in others the direct evidence of such fibres is slight or absent.

4. The Vth. thoracic appears occasionally to have a few accelerator fibres, but further evidence is desirable.

5. The VIth. may perhaps occasionally have a few accelerator fibres, but at present this must be regarded as very doubtful.

It may be noted that in Cat (7), the Vth. and VIth. thoracic nerves, when stimulated after an interval of rest, caused the heart to take wider excursions, as if beating more strongly, this effect might or might not be accompanied by a slight slowing; when the nerve was stimulated several times, say at intervals of $1\frac{1}{2}$ or 2 minutes, this effect on the heart rapidly disappeared, although the rise of blood-pressure remained much the same.

Stimulation of the lower cervical nerves, instead of causing acceleration, usually caused a slowing or irregularity in the heart-beat; this was probably brought about, indirectly, by the strong muscular contraction.

It will be noticed that the origin of the accelerator nerves very closely corresponds —and may possibly be identical—with the origin of the vaso-motor fibres for the head. I must confess that I had expected the origin of the cardiac nerve-fibres to be several segments lower than that of the nerve-fibres to the auricular artery.

I have made one or two experiments on the Dog to determine the position of the nerve-cells with which the accelerator fibres are connected. In these experiments the rami communicantes of the upper thoracic nerves, the ganglion stellatum, the nerves running from the ganglion stellatum, the inferior cervical ganglion and the nerves running from it, were stimulated before and after application of 1 per cent. nicotin to one or both ganglia. The experiments were not altogether satisfactory, since after opening the chest there was some inconstancy in the action of the nerves before nicotin was applied to the ganglion. On the whole, however, they were decidedly in favour of some accelerator fibres being connected with nerve-cells in the ganglion stellatum, and others with nerve-cells in the inferior cervical ganglion.

The Origin of the other Fibres of the Cervical and Upper Thoracic Sympathetic.

A few words may be said about these for the sake of completeness.

Pilo-Motor Nerve-Fibres.—Sherrington and myself* have shown that in the Ape the pilo-motor fibres for the cervical sympathetic arise from the IInd. to the Vth. thoracic nerves inclusive, and in the Cat from the IIIrd. or IVth. to the VIIth. thoracic nerves inclusive.

* Langley and Sherrington, 'Journal of Physiology,' vol. 12, p. 278, 1891.

In my further experiments on the Cat, I have, as a rule, looked for the effect on the hairs. Whilst the movement of the hairs on the face and upper vertebral area was always more or less distinct on stimulating the IVth., Vth., and VIth. nerves, I have not observed any second instance in which the IIIrd. nerve was effective.

The hairs over the last two or three cervical vertebræ and the first one or two thoracic vertebræ are innervated by fibres which pass through the ganglion stellatum, but their exact origin I have not yet determined.

I have also found pilo-motor fibres in the Dog in the cervical sympathetic, but, so far, for the dorsal part of the neck only, and not for the face. They arise from the IVth., Vth., and VIth. thoracic nerves; nerves below this I have not yet tried. The IVth. has less action than the Vth. and VIth. thoracic nerves.

Sweat Nerves to the Fore-feet.—These* leave the cord by the IVth. to IXth., and occasionally by the Xth. thoracic nerves, the greatest number usually passing out by the VIIth.

Vaso-motor Nerves for Fore-feet.—Bradford and Bayliss† have shown that they leave the cord by the IVth. to the Xth. thoracic nerves inclusive; perhaps there may occasionally be some vaso-motor fibres for the foot in the IIIrd. thoracic also.†

Vaso-motor Nerves for Lungs.—According to Bradford and Dean,‡ vaso-motor nerves for the lungs arise from the IInd. to the VIIth. thoracic nerves inclusive. Knoll,§ however, does not consider the proof of the existence of these nerves as satisfactory.

Vaso-motor Nerves for the Abdominal Viscera.—The highest nerve from which these are given off has not been determined, but some observers have stated that the fibres of the splanchnic nerve could be traced as high as the IIIrd. thoracic; the rise of blood-pressure produced in favourable circumstances by stimulating the IIIrd. and IVth. thoracic certainly suggests that these nerves may send fibres to the viscera. Bradford,|| however, did not find any satisfactory proof of vaso-motor fibres for the kidney above the VIth. thoracic nerve.

* Langley, 'Journal of Physiology,' vol. 12, p. 366, 1891.

† *Cf.* Langley, 'Journal of Physiology,' vol. 12, p. 377, 1891.

‡ Bradford and Dean, 'Roy. Soc. Proc.,' vol. 45, p. 369, 1889. With regard to some of these nerves, the statements are rather conflicting; thus, the Authors say that when the VIth. and VIIth. thoracic nerves are stimulated "the pulmonary rise, although considerable, ... is not out of proportion to the aortic rise," further that "no very definite results have been obtained by stimulating the IInd. dorsal nerve."

§ Knoll, 'Sitzungsb. d. Wiener Akad., Math.-naturw. Cl.,' vol. 99, Abt. 3, p. 5, 1890.

|| Bradford, 'Journal of Physiology,' vol. 10, p. 358, 1889.

Some Remarks upon the preceding Observations.

The foregoing experiments have shown that in the Rabbit, Cat, and Dog, the cervical sympathetic arises from the first seven thoracic nerves at least; and that in the Rabbit it receives a few fibres from the eighth thoracic nerve. But this similarity in extent of origin in the three animals is somewhat superficial, for the VIth. and VIIth. thoracic nerves are represented in the cervical sympathetic of the Rabbit by vaso-motor fibres, whilst in the Cat and Dog they are represented by pilo-motor nerve-fibres;—a class of nerve fibre which appears to be absent in the Rabbit.

Comparing the Rabbit with the Cat and Dog as regards sympathetic nerve-fibres which are present in all, we find that in the Cat and Dog the sympathetic fibres of any one kind are higher in origin, and in some cases are present in fewer spinal nerves than they are in the Rabbit. Thus in the Cat and Dog, the Ist. thoracic nerve has a strong and the IIIrd. thoracic has a slight pupillo-dilator action, whilst in the Rabbit the action of the IIIrd. thoracic nerve is usually greater than that of the Ist. So, too, in the Cat and Dog, the vaso-motor fibres stretch—broadly speaking—from the Ist. to the Vth. thoracic nerves inclusive, whilst in the Rabbit they extend from the IInd. to the VIIIth. thoracic nerves inclusive. It is in harmony with this that in the Rabbit the IInd. thoracic always, or nearly always, sends motor fibres to the fore foot, whilst in the Cat and Dog the lowest motor fibres for the fore foot commonly proceed from the Ist. thoracic nerve.

Differences like these between the Cat and Dog on the one hand, and the Rabbit on the other, exist also, though only to a slight extent, between the Cat and the Dog. Generally speaking, in the Dog, the nerve-fibres of any one kind are a trifle higher in origin than in the Cat.

There is another point deserving of notice. If we consider the various actions of the first seven thoracic nerves in the Cat, noting by which nerves the maximal actions are produced, we find that each nerve except the IVth. can produce an effect on some tissue which is not exceeded by that produced by any other nerve. Thus:

I. Maximal effect on the pupil.

II. Maximal effect on pupil, eye, secretion, sometimes acceleration of heart, and perhaps sometimes on blood-vessels of head.

III. Maximal effect on blood-vessels of head, and sometimes on acceleration of heart.

IV.

V. Maximal effect on hairs of face and neck.

VI. Maximal effect on hairs of face and neck; and occasionally on sweat glands of fore foot.

VII. Maximal effect on sweat glands of fore foot.

This gap in the series cannot, so far as our present information goes, be filled up by Bradford and Dean's vaso-motor fibres for the lungs, for they find that the IIIrd.

thoracic has a greater effect than the IVth., and—to judge from one passage—that the IInd. has more effect than the IIIrd.

REMARKS ON THE WHITE AND GREY RAMI COMMUNICANTES.

I have in the preceding sections dealt with the origin from the spinal cord of various classes of sympathetic nerve-fibres in a particular region of the sympathetic system. The fibres proceeding from the cord to the sympathetic can only pass by the rami communicantes, and as there are two kinds of rami communicantes, one consisting mainly of medullated, and the other mainly of non-medullated nerve-fibres, we are naturally driven to consider—especially in the light of GASKELL's work quoted below—whether the nerve-fibres with which we have been dealing pass by one only or by both of these. A full account of the previous work on the white and grey rami is not necessary here; it will be sufficient to mention one or two of the chief observations.

BECK,* in 1846, in a paper on the nerves of the uterus, stated as the result of dissecting and teasing nerves in Man, that the white rami consisted of "tubular," *i.e.*, of medullated fibres which arose from the spinal cord, passed from it in the anterior and posterior roots, and then ran peripherally chiefly in the splanchnics and other similar nerves. These "tubular" fibres had, he considered, no connection with the "corpuscles" of the sympathetic ganglia. The grey rami consisted almost altogether of "gelatinous," *i.e.*, of non-medullated fibres which had their origin in the "corpuscles" of the sympathetic ganglia. The grey rami thus ran from the ganglia to their peripheral distribution; a few "gelatinous" fibres could be seen in the anterior and posterior roots, but these BECK thought supplied the blood-vessels of the spinal cord. The scarce "tubular" fibres in the grey rami he considered to be fibres which had left the spinal cord by the white rami.

The experiments of BUDGE and WALLER and of many others showed that all the effects which can be produced by stimulating the sympathetic in any region can be produced by stimulating the spinal nerves in the vertebral canal, or by stimulating the cord itself. In consequence of these observations, and of the progress of histological knowledge regarding the ganglion cells, it became probable, though by no means proved, that efferent sympathetic nerve-fibres were simply cerebro-spinal nerves having one or more nerve-cells on their course. This view was advocated by GASKELL.†

Both BECK and GASKELL describe the grey ramus as a nerve-bundle running from the sympathetic chain to peripheral endings in blood-vessels or other structures. And both do so on similar grounds. BECK followed the grey rami by dissection and teasing, GASKELL by cutting serial sections. According to GASKELL all the non-medullated fibres which pass from the grey rami centrally, run

* BECK, 'Phil. Trans.,' 1846, p. 213.

† GASKELL, 'Journal of Physiology, vol. 7, 1886, p. 1.

to the membranes of the spinal cord, and do not enter it with the anterior and posterior roots.

So far, then, what may be regarded as shown is that only medullated fibres run from the spinal cord to the sympathetic chain, and that the white rami contain very many medullated fibres whilst the grey rami contain very few. The asserted sharp distinction between white and grey rami stands, however, on a different footing. So far as concerns their histological characters, the difference between them is rather one of degree than of kind, they both contain medullated fibres of various sizes, and non-medullated fibres. The principal unknown points are the nature and course of the medullated fibres of the grey rami. It is probable that they course peripherally with the non-medullated fibres of the rami, for each grey ramus divides as, or before, it reaches its spinal nerve, and part runs peripherally with the nerve, and part runs towards the spinal cord; it is reasonable to suppose that the medullated fibres in the two parts have similar functions, and since those in one part run peripherally, so presumably do those in the other.

As GASKELL has pointed out, the question of the connections of the white and grey rami may be attacked from the side of physiological experiment, as well as from that of histological observation. Some nerves have both white and grey rami, others have grey only. A preliminary point to make certain of in this line of inquiry is the distribution of the white and grey rami. BECK's description for Man, is that white and grey rami communicantes are present in the thoracic and lumbar regions; in passing down the lumbar region the white rami become smaller, and the grey rami larger; in the pelvic region grey rami only are present.

ÓNODI* gives a similar description for the Horse. GASKELL made observations on the Dog; he found that the rami communicantes of the lower cervical and Ist. thoracic nerves were grey only. The uppermost white ramus came from the IInd. thoracic, the lowermost white ramus was from the IVth. lumbar nerve.† Below this, grey rami only were present.

I have examined the white and grey rami in the Dog, Cat, and Rabbit.

The uppermost white ramus I find to be in all cases given off by the Ist. thoracic nerve. I have given more attention to this in the Cat and Dog than in the Rabbit. In dissecting in the Cat and Dog, the uppermost *obvious* white ramus is that from the IInd. thoracic; but with a little trouble one, two, or three fine white strands can be seen stretching from the Ist. thoracic nerve to the ganglion stellatum. When these are hardened in osmic acid and sections cut, they are seen to have the characters of white rami, that is, they consist chiefly of small medullated fibres collected in bundles,

* ÓNODI, 'Arch. f. Anat. u. Physiol.' (Anat. Abt.), p. 145, 1884.

† GASKELL speaks of this as the IInd. lumbar nerve—giving the Dog 15 thoracic instead of 13—in order that the corresponding lumbar and sacral nerves in the Dog and Man may have the same numbering. I do not, however, think that this method attains its object, so that I prefer to count the thoracic nerves according to the number of ribs.

with a few medium and medium-large fibres; between the bundles are a variable number of non-medullated fibres; besides these there are one or more grey rami, *i.e.*, bundles consisting chiefly of non-medullated fibres, but containing scattered medullated fibres. In three out of the four cases in which, in the Dog, the tissue between the Ist. thoracic nerve and the ganglion stellatum was hardened and cut, there was more than one white ramus, in other nerves there is occasionally more than one white ramus, and the IIIrd. lumbar nearly always, if not always, has two, easily seen with the eye. In one case I counted roughly the number of small medullated fibres in the rami of the Ist. thoracic nerve, and found about 500 to be present.

As regards the position of the lowermost white ramus, I agree in the main with GASKELL. As a rule, both in Dog and Cat, the lowermost white ramus is given off by the IVth. lumbar nerve; the ramus runs to, or nearly to, the Vth. lumbar sympathetic ganglion; sometimes, however, there is a white ramus to the VIth. lumbar sympathetic ganglion, arising, apparently, from the Vth. lumbar nerve; but it is possible that this ramus is really brought to the Vth. nerve by the descending branch of the IVth. Further, in the two cases in which I have noticed an additional nerve in the dorso-lumbar region in the Cat,* the last white ramus was from the Vth. and not from the IVth. lumbar nerve; in both of these cases, the Vth. lumbar nerve was, I think, in the main homologous with the IVth. lumbar nerve of the normal animal. In the Rabbit, the lowermost white ramus is, as a rule, from the Vth. lumbar nerve; this corresponds to the IVth. lumbar of the Cat and Dog.

We may now consider the bearing of the experiments on stimulating the nerves in the spinal canal upon the question of the nature of the medullated fibres in the grey rami. In the first section of this paper, it has been shown that no trace of any one of the effects which can be produced by stimulating the upper thoracic nerves and the cervical sympathetic, can be produced by stimulating the lower cervical nerves. That is to say, the medullated nerve-fibres which are present in the grey rami of the lower cervical nerves, are either not efferent fibres, or they are too few to produce any perceptible effect.

The Ist. thoracic spinal nerve, the uppermost nerve which has a white ramus, is the uppermost nerve which on stimulation produces sympathetic effects.

I have also made a considerable number of experiments in the Cat and Rabbit upon the stimulation of the lumbar nerve-roots, as many as possible of the sympathetic effects being observed. In the Cat, the IVth. lumbar was in all cases, save one, the lowermost nerve which caused any sympathetic effect. The exception occurred in one of the Cats spoken of above, in which there was an extra lumbar nerve, and an extra white ramus. In the Rabbit the Vth. lumbar was in all cases the lowest from which a sympathetic effect could definitely be obtained. Thus in the lower lumbar, as in the lower cervical, no indication could be obtained that the

* 'Journal of Physiology,' vol. 12, p. 351, 1891.

medullated nerve-fibres in the grey rami are efferent fibres proceeding from the sympathetic trunk.

Putting this view on one side, we may pass on to consider some other possibilities with regard to the function of the medullated fibres in the white and grey rami.

BIDDER and VOLKMANN* considered that all medullated fibres could be divided into two classes, differing in histological characters. They differed also in size, and were separable from one another by the excessive scarcity or, in some instances, by the complete absence of fibres of intermediate size. On the basis of observation as to the relative number of these two classes of fibres in various typical nerves of the body, they came to the conclusion that the smaller nerve-fibres belonged to the organic or vegetative functions of the body, and that the larger nerve-fibres were concerned with its psychical activities. The former they called "sympathetic," the latter "cerebro-spinal" nerve-fibres. The scattered cerebro-spinal fibres found in the trunk of the sympathetic and its branches they considered to be sensory fibres. The measurements given by BIDDER and VOLKMANN are in terms of the Paris inch; in the sympathetic of the Cat the measurements given—taking ·00001 Paris inch = ·0002707 mm.—are 11·9 μ for the smallest and 17·9 μ for the largest cerebro-spinal nerve-fibres, and 4·1 μ for the smallest and 5·4 μ for the largest sympathetic fibres. In other nerves, fibres of greater diameter than 5·4 μ are included in the class of sympathetic fibres; thus fibres of 5·9 μ in the IIIrd. nerve of the Cat, and fibres of 6·7 μ in the skin nerves of Man.

These views received very little support until GASKELL'S work in 1886. GASKELL concerned himself with efferent visceral fibres only; he compared the function and the histological characters of a considerable number of nerves, and pointed out that in all these cases the nerves which had visceral functions contained many small nerve-fibres, so that there was good ground for believing that efferent visceral nerves are always small. GASKELL gives 1·8 to 3·6 μ as the diameter of these nerve-fibres.

The theory of BIDDER and VOLKMANN, that the large fibres of the sympathetic system are fibres of general sensibility, seemed to me, at first sight, as satisfactory as it was simple, and I was the more inclined to adopt it because of some facts connected with the cervical sympathetic. BUDGE and WALLER found that stimulation of the cervical sympathetic in an unanæsthetised Rabbit caused no sign of pain. I have on several occasions made special experiments on the anæsthetised Rabbit and Cat, with the object of determining whether stimulation of the central end of the cervical sympathetic causes a reflex of any kind. I have not observed any certain reflex, neither body movement, nor variation of blood-pressure, nor change in rate of respiration or heart-beat, nor alteration in the pupil or arteries of the opposite side of the head. On microscopical examination the cervical sympathetic is sometimes found to be destitute of any medullated fibre larger than 4 μ. Most of the medullated fibres are 2·2 μ to

* BIDDER and VOLKMANN, 'Die Selbständigkeit des Sympathischen Nervensystems' (Leipzig), 1842.

3·5 μ, and there are also non-medullated fibres; sometimes—and this was described by BIDDER and VOLKMANN—there are a few larger fibres, viz., three to six fibres, about 5·5 μ, and two or three, about 11 μ in diameter. These fibres, however, are probably derived from the vagus, and run downward, for after section of the cervical sympathetic I have found, some weeks later, a group of six to eight similar fibres just inside the sheath of the superior cervical ganglia.

Notwithstanding the striking corroboration of BIDDER and VOLKMANN's theory, which is afforded by these facts, further inquiry shows, I think, that in the main it is erroneous.

Before proceeding with this inquiry, it will be convenient to give some observations on the size of the medullated fibres in the grey rami and in the rest of the sympathetic system.

When a piece of a ramus communicans, or of the trunk of the sympathetic down to the Ist. sacral ganglion, or of one of the branches running to the solar plexus, or to the inferior mesenteric ganglion is teased out, after having been treated with osmic acid for a day, three sizes of medullated fibres at once catch one's attention. The fibres are about 3 μ, 5 μ, and 8 μ respectively. Occasionally in the branches of the sympathetic, and more frequently in the trunk of the sympathetic and in the white rami, there are fibres 10 μ to 12 μ in diameter. In examining the several strands of a teased-out piece of nerve, I have rarely felt any hesitation as to which of the three classes each fibre belonged to, the fibres of about 5 μ and 8 μ are markedly different from the rest by the obviousness of the medullary sheath. But on measuring all the fibres of greater diameter than 3·8 μ, it is found that the gaps between the different classes are very slight,* and on including in the measurement fibres from different parts of the sympathetic system, all sizes may be found from 2 μ to 12 μ. It will be remembered that SCHWALBE,† in his tables of the size of the nerve fibres in the roots of the spinal nerves of the Frog, gives no break in size corresponding to that described by BIDDER and VOLKMANN. The matter, however, requires further careful investigation.

The general appearance of white and grey rami treated with osmic acid and cut transversely is depicted by GASKELL. I may add some further points of detail. In the white rami there are, in most cases, more fibres larger than 4 μ than are shown in the particular white ramus figured by GASKELL. In the grey rami both the total number of medullated fibres, and the relative number of the 3 μ, 5 μ, and 8 μ types vary. The cervical have fewer medullated fibres than the lumbar grey rami, and the VIIth. lumbar has fewer than the VIth.; in the VIth. lumbar grey ramus of the Dog there are fifteen to twenty fibres above 4 μ in diameter. The majority of the medullated fibres are in the peripheral part of the rami. The number of small medullated fibres

* Some of the nerves of intermediate size, probably arise from the division of the larger nerves.

† SCHWALBE, 'Ueber die Kaliberverhältnisse der Nervenfasern' (Leipzig), 1882.

in the corresponding grey rami of different animals appears to me to vary considerably. Whilst making experiments upon the effects of stimulating the lower lumbar sympathetic, I usually teased out the grey rami, either fresh or in osmic acid; in some cases I found large numbers of small medullated nerves. It is true that in the grey rami, which I have since hardened and cut, the small medullated fibres have been scattered and few, varying from about ten to twenty-five; but their occasional presence in quantity, in circumstances which do not seem to me to leave open any source of error, leads me to doubt whether a medullated fibre, after passing through a sympathetic cell—using this expression for convenience—is necessarily non-medullated. And this doubt is strengthened by some other facts. In the Frog, the rami communicantes of the lower lumbar nerves consist almost entirely of medullated nerves, and I do not find any grey rami; most, at any rate, of these medullated fibres are connected with nerve-cells in the sympathetic ganglia. Further, it will be remembered that BIDDER and VOLKMANN described the short ciliary nerves as being free from interstitial tissue, *i.e.*, from non-medullated fibres, so that the small medullated nerve-fibres pass through the ciliary ganglion without losing their medulla—a fact which has been confirmed by several observers, and recently by GASKELL.

Whilst speaking of the loss of medulla by a nerve, there is another point it is, perhaps, worth while to mention. It is very commonly assumed that sympathetic nerve-fibres, after being connected with nerve-cells in any one sympathetic ganglion, pass on and are again connected with nerve cells in one or more sympathetic ganglia. This view has been taken for various reasons, and, amongst others, because ganglion cells are found in the course of non-medullated fibres. The real explanation of this fact is, I think, that the nerves sometimes lose their medulla a considerable distance before they become connected with nerve-cells. This explanation receives some confirmation from what I have said above as to the variability in the medullation of the fibres of the grey rami. The experiments I have published upon the connection of nerve-fibres with nerve-cells, based upon the action of nicotin, give, I think, strong ground for concluding that any one sympathetic nerve-fibre passes into a nerve-cell in one sympathetic ganglion only.

It is sometimes said that medullated fibres cease in the lower lumbar, or in the upper sacral region. I do not find this to be so in either the Dog, Cat, or Rabbit. In the cases I have examined, a few medullated fibres were found down to the last sympathetic ganglion; in the Dog there are a considerable number above the Ist. sacral ganglion. From the IInd. sacral ganglion downwards, there are but few in all three animals, but fewest in the Rabbit. Thus, in one case, the sympathetic between the IInd. and IIIrd. sacral ganglia contained eight medullated fibres only—seven small, and one of medium size The number of nerve-cells below this region is, of course, very considerable.

The lower lumbar and upper sacral region is particularly adapted for experiments to determine whether the grey rami contain sensory fibres, and, if so, in which direction they run, since in this region there are no white rami.

The first point to settle was whether afferent fibres run from the sympathetic to the spinal cord by the grey rami. If the sympathetic trunk in an anæsthetised Cat be laid bare from the Vth. lumbar ganglion to the IInd. sacral, and any part of it be stimulated, a reflex movement, and still more readily a rise of blood-pressure is

obtained*, *i.e.*, afferent fibres leading to these effects are present throughout this region. If, then, the sympathetic be cut just below the junction of the last white ramus with it, and the sympathetic be stimulated below the point cut, there is no longer a reflex movement, and usually no rise of blood-pressure†; hence, none of the afferent fibres just spoken of enter the spinal cord by the grey rami of the VIth. and VIIth. lumbar, or of any lower nerve, and it can easily be shown that these afferent fibres pass to the cord by the white rami. Thus, if the sympathetic trunk be cut between the IInd. and IIIrd. lumbar ganglia, a reflex movement and a rise of blood-pressure is obtained by stimulating the sympathetic in the sacral region, and this effect is obtained, in a more or less marked degree, as long as any one of the white rami below the point of section of the sympathetic remains intact.

A modification of the experiment with the grey rami may be made by tying and cutting one of them as close as possible to the sympathetic trunk, isolating it, and stimulating the end connected with the spinal nerve. In the Cat, this is, as a rule, most easily done with the ramus of the Ist. sacral nerve. Since the ramus is about a centimetre only in length, the interrupted current used must not be too strong, and careful observation must be given to any indication of an escape of current. In such experiments, I have not been able to observe a reflex action of any kind. Peripheral effects are obvious, such as secretion of sweat and erection of hairs, but there is no body movement, no variation of blood-pressure,‡ no dilation of the pupils, and, in short, no signs of any reflex effects.

The next point to attempt to determine was whether the grey rami contain afferent fibres passing not to the spinal cord, but to their peripheral endings. It is known that a grey ramus runs in part centrally and in part peripherally in its spinal nerve. If, then, the grey ramus contains afferent fibres of general sensibility in both its branches, stimulation of (*a*) the peripheral end of a spinal nerve, cut in the vertebral canal, and (*b*) of the central end of a spinal nerve after it has been cut in the vertebral canal, should cause a reflex body movement. I am not aware of any evidence of such a reflex action, and it is unlikely that if it occurred it should have escaped notice. In numerous experiments upon anæsthetized Cats, I have looked for a body movement other than that occurring in the peripheral area of the nerve stimulated, and have never been able to satisfy myself that any reflex body movement took place. And stimulation within the spinal canal of the nerves which do not contain vaso-motor fibres, such as the lower cervical and lower lumbar nerves, causes, when curari also has been given, no variation of blood-pressure.

* The reflex effects decrease in passing downwards.

† Occasionally a slight variation of blood-pressure may be observed, probably due to the stimulation of the vaso-motor fibres of the limb, for it is abolished by cutting the nerves to the limb, peripherally of the grey rami.

‡ Under especially favourable conditions, it is probable that the vascular effects caused by stimulating the grey ramus of the VIIth. lumbar, or of the Ist. sacral nerve, would cause a slight variation of arterial blood-pressure, but I have not observed any.

In other experiments the spinal nerves which give origin to the sciatic were cut in the spinal canal, the sciatic tied and cut in the leg, and its central end stimulated. No effect was observed. The sciatic was then isolated up to its origin in the lumbo-sacral plexus, and these origins stimulated, without effect; lastly the Ist. sacral nerve as it joined the lumbo-sacral plexus was ligatured, cut, and isolated with its grey ramus, the grey ramus remaining attached to the Ist. sacral sympathetic ganglion; stimulation of the grey ramus was without effect until the electrodes were almost touching the ganglion, that is, until there was in all probability an escape of current to the sympathetic chain.

I have also tried in the Dog a similar experiment with the grey rami; the VIth. and VIIth. lumbar nerves were cut centrally and peripherally of the grey rami, the grey rami isolated, and stimulated. The grey ramus of the VIIth. nerve had no appreciable effect on movement, blood-pressure, or respiration; the grey ramus of the VIth. sometimes caused a slight twitch of some lumbar muscle, and a slight effect on the blood-pressure and respiration; but as these effects were very marked when the adjacent VIth. lumbar sympathetic ganglion was stimulated, the effects observed on stimulating the grey ramus may have been due to an escape of current to the sympathetic trunk.

Actual experiment, then, gives very little support to the view that there are afferent fibres in the grey ramus. On the other hand it is in the highest degree improbable that the large medullated fibres should be efferent fibres; every visceral efferent effect can be fairly attributed to small medullated fibres, and no single visceral efferent effect can, at present, with any probability be attributed to fibres above 4 μ in diameter; further, as is well known, the Pacinian bodies of the mesentery of the Cat are supplied with fibres arising from the division of large medullated fibres.

Assuming, then, notwithstanding the experimental evidence, that the medium and large fibres in the grey rami are afferent fibres, we have two possibilities to contemplate, (1) they may be ordinary fibres of general sensibility, but too few in number to produce on electrical stimulation, and in the conditions of the experiment, the customary reflex actions of such fibres.

With regard to this there are several points to consider.

I do not think that the failure to produce an effect could have been due to the general conditions of the experiment; for concurrently with my observations on the grey rami, I made also experiments on the white rami, and even with the smallest white ramus I have never failed to obtain a reflex movement of the body and a rise of blood-pressure.

It is well known that sensory fibres are contained in the annulus of VIEUSSENS, in the splanchnic, and in the branches from the lumbar sympathetic to the inferior mesenteric ganglia, and that the white ramus arises from the posterior as well as from the anterior roots. Consequently, there was practically no doubt that the white rami contained sensory fibres for the sympathetic system. Still, partly for the sake of completeness and partly to serve as a control in stimulating the grey rami, I have

in various experiments stimulated each white ramus, except those in the lower thoracic region. The ramus may, in a good many cases, be tied, cut, and its central end stimulated; in other cases, it is easier and more satisfactory to tie the sympathetic above and below the ramus, isolate the portion of the sympathetic between the ligatures, cut the grey ramus, if one is present, and stimulate each end of the sympathetic. I have said that the uppermost white ramus is that running from the first thoracic nerve to the ganglion stellatum. I have observed the presence of sensory fibres in this in the following way:—The connections of the ganglion stellatum were cut, with the exception of the white ramus, to the 1st thoracic nerve and the two limbs of the annulus of VIEUSSENS, the limbs of the annulus of VIEUSSENS were tied, cut, and stimulated near the ganglion stellatum.

I have mentioned above that stimulation of the peripheral ends of the spinal nerves in the spinal canal does not cause any perceptible reflex action, but it can hardly be doubted that sensory nerves are distributed to the sheaths of the spinal nerves; and it may be said that the result shows that, in fact, the electrical stimulation of a few sensory fibres does produce no perceptible reflex effect. But this argument involves the assumption that the sheath of each spinal nerve does not receive its sensory supply through its own posterior root—an assumption which, so far as I know, is unfounded, and which is at variance with some of the facts upon which the view of "recurrent sensibility" is founded.

Some direct evidence against the view that all the large medullated fibres are fibres of general sensibility of the sympathetic system, is afforded by comparing the degree of sensitiveness of different parts of the sympathetic with the number of large fibres in them. I have taken thus the splanchnics, the homologous nerves running to the inferior mesenteric ganglion, the hypogastric nerves, the lower lumbar and the sacral sympathetic trunk, and the lumbar grey rami; and I do not find any satisfactory correspondence between the readiness with which the nerves give a reflex body movement or variation of blood-pressure and the number of large fibres, or of fibres of greater diameter than 4 μ, contained by them. Further, the nervus erigens, a nerve of a high degree of sensitiveness, contains in the Rabbit a few fibres only larger than 4 μ.* One other observation bearing on this point may be mentioned. Whilst stimulating the central end of the annulus of VIEUSSENS, in order to ascertain from which nerve-roots the sensory fibres of the two branches arose, I found that a branch of the posterior limb of the annulus, running to the vagus, produced a reflex far more readily than all the rest of the annulus put together. This branch was hardened in osmic acid and cut, and no single fibre larger in diameter than 4 μ was found in it.

(2) The second possibility to consider is that many of the large fibres, and to a varying extent in different nerves, are afferent fibres of some special sense, or subserve local visceral reflexes which escape attention under the conditions of the experiment. This view seems to me the most probable one. Some light is thrown on it by considering the depressor nerve. It is well known from the work of LUDWIG and CYON and others that this nerve causes a reflex fall of blood-pressure, and some-

* The nervus erigens usually has one or two fibres 12 to 14 μ in diameter.

times a slowing of the heart-beat, but does not cause a reflex movement. In the Rabbit and Cat I have first stimulated the depressor in order to be certain of what reflexes it was capable of giving, and then I have examined the nerve microscopically. Either teased out or in transverse sections it forms a striking contrast to the cervical sympathetic on account of the number of fibres with deeply-stained distinct medulla, and diameter varying from 4 μ to 8 or 10 μ, which it contains.* Since in all cases the depressor caused no reflex movement and gave no sign of containing fibres of general sensibility, it is fairly certain, I think, that in this nerve at any rate the larger nerve-fibres are not nerves of general sensibility.

I conclude, then, that the medullated fibres of larger diameter than 4 μ, which occur in the grey rami, are afferent fibres entering the cord by the white rami, but are not for the most part fibres of general sensibility. It seems to me probable that the afferent fibres of general sensibility are not fibres of any given diameter, but a further consideration of this question is beyond the scope of the present paper.

Explanation of Plates.

PLATES 9, 10.

The figures are diagrams to illustrate the origin from the spinal cord of the different kinds of nerve-fibres dealt with in the text. I. to X. represent the first to the tenth thoracic spinal nerves respectively. The curved line (*wh.r.c.*) represents the white ramus communicans.

th.sy. = thoracic part of sympathetic.
c.sy. = cervical sympathetic.
s.c.g. = superior cervical ganglion.
g.st. = ganglion stellatum.

It will be noticed that in any one figure the white rami are of different thicknesses; this is to represent roughly the different degree of effect produced by stimulating the corresponding spinal nerve, so that the thicker the ramus the more fibres of the especial kind under consideration pass by it to the sympathetic. An accurate estimation of the number of fibres of each kind which pass by the several rami is of course at present out of the question. Further, the representation of the number of fibres in the rami of any one figure is not intended to be compared with the representation of the number of fibres in the rami of any other figure.

When a ramus is represented by a broken line it indicates that a few fibres are sometimes, but apparently not always, present; when a ? is added, it indicates that

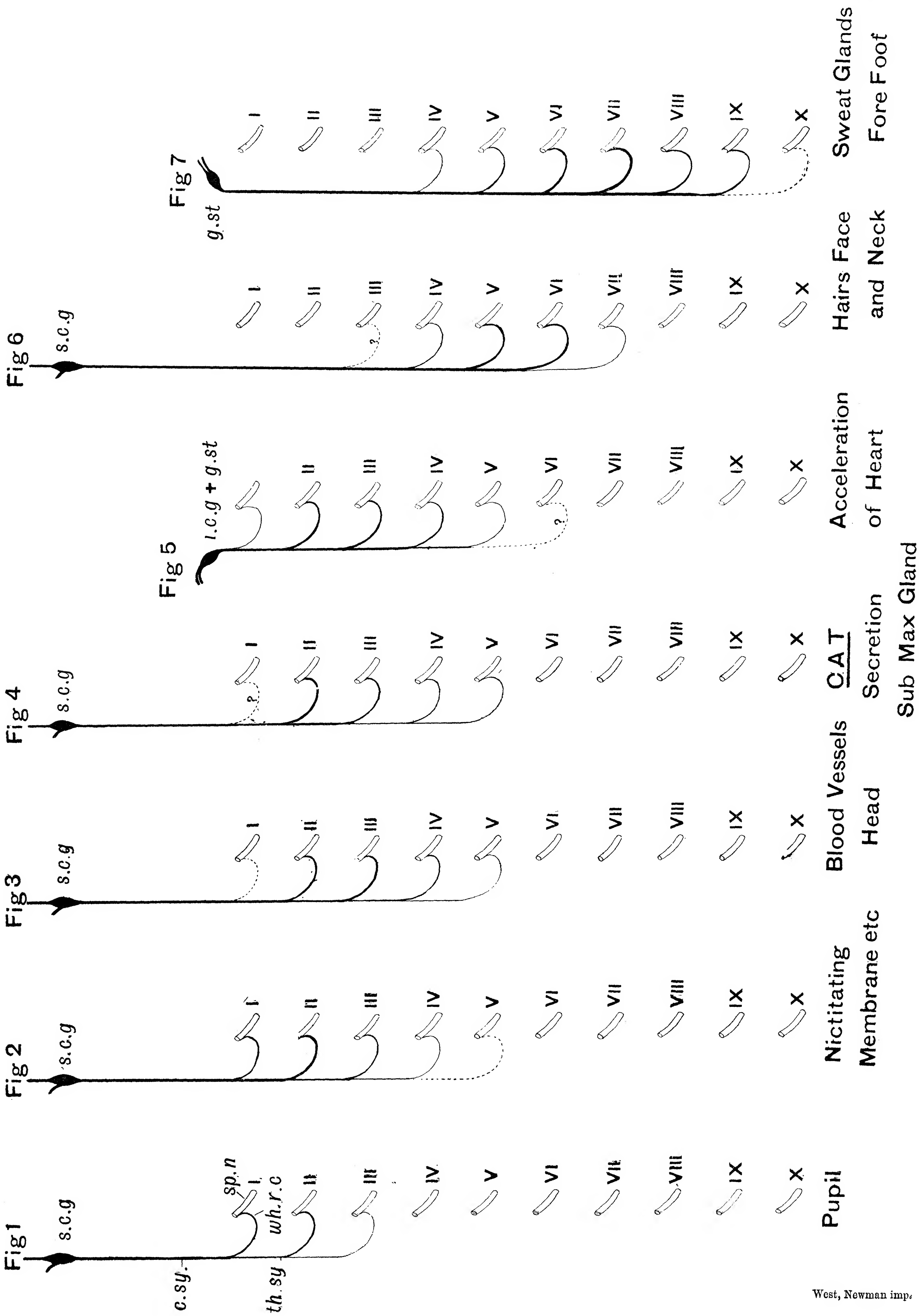
* In the Rabbit the depressor consists of a few fibres 8 to 10 μ, about 30 fibres of diameters between 7 and 4 μ, and a variable number of small medullated and non-medullated fibres.

a few fibres are apparently sometimes present in this ramus, but that further evidence is required.

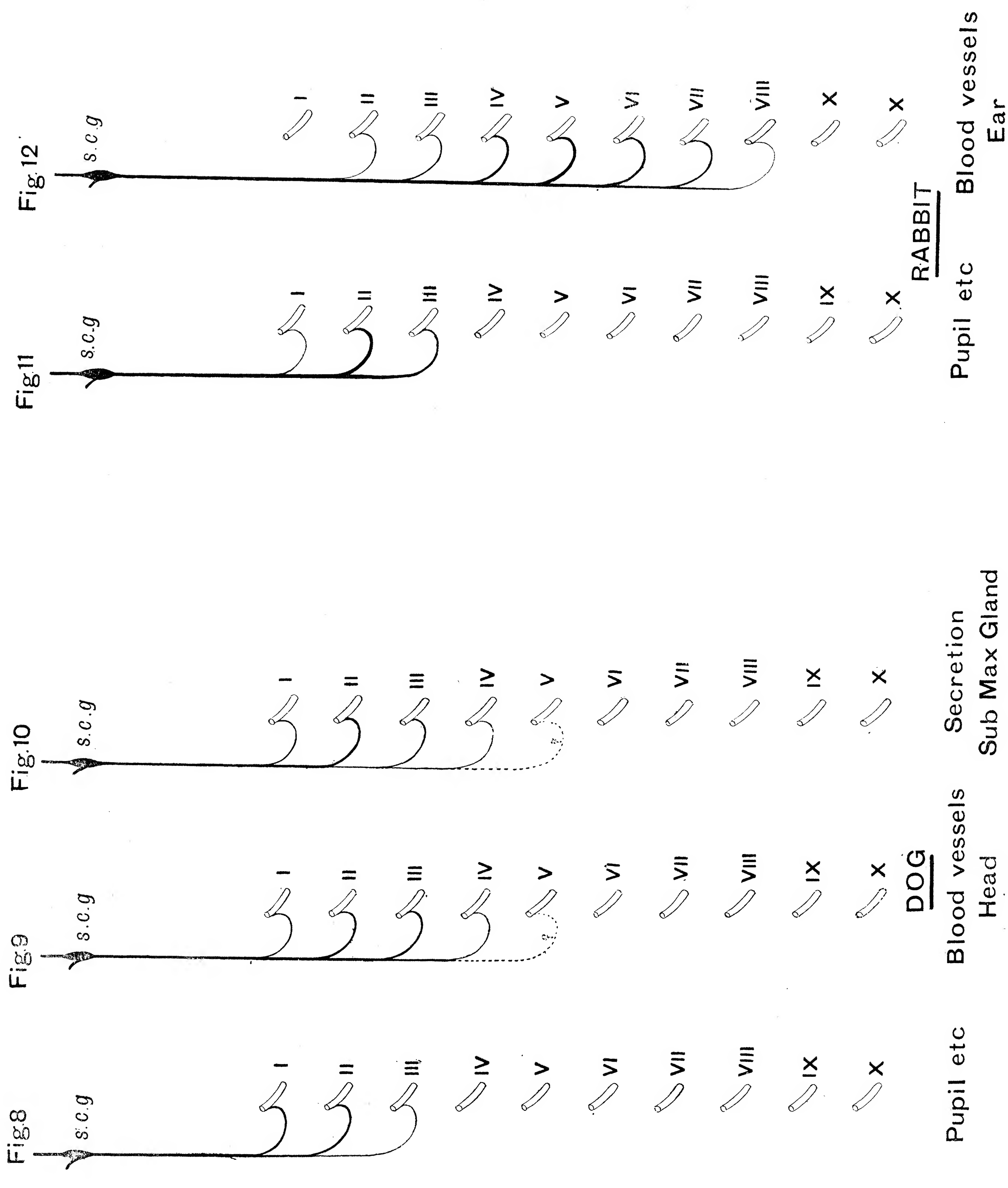
I have also inserted the sympathetic ganglion in which I consider that the nerve-fibres in each particular case become connected with nerve-cells. Thus all the fibres of the first four figures are, I think, connected with nerve-cells in the superior cervical ganglion, and nowhere else, except for a few aberrant cells properly belonging to this ganglion. In Fig. 5 the inferior cervical ganglion (*i.c.g.*) and the ganglion stellatum (*g.st.*) are represented as one; probably a part of the accelerator fibres end in the one ganglion, and the rest in the other.

Fig 2 represents the origin of the fibres which cause withdrawal of the nictitating membrane, separation of the eyelids, protrusion of the eye.

Fig. 8 and Fig. 11.—'Pupil, etc.,' indicates that the fibres leading to the various effects just mentioned have the same origin as those leading to the dilation of the pupil.



West, Newman imp.



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